AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 110:17–25 (1999)

Fatal Attraction: Interest in Infants and Infant Abuse in Rhesus Macaques

DARIO MAESTRIPIERI*
Yerkes Regional Primate Research Center, Emory University, Lawrenceville, Georgia 30043

KEY WORDS maternal behavior; infant handling; infant maltreatment; competition; primates

ABSTRACT This study investigated whether infant abuse by female rhesus macaques (*Macaca mulatta*) is a phenomenon specific to their own offspring or reflects a general tendency to interact negatively with infants. Several aspects of the relationship between maternal behavior, infant handling, and infant harassment were also investigated. Study subjects were 20 group-living rhesus mothers with their infants observed during the first 12 weeks of lactation. The results of this study indicate that abusive mothers are highly attracted to infants in general but that infant abuse is a phenomenon specific to their own offspring. Infant harassment is not an accidental by-product of infant handling or the result of maternal inexperience but it is likely related to reproductive competition among lactating females. Maternal behavior and infant handling may be regulated by similar proximate mechanisms, but probably have different adaptive functions and evolutionary history across the Primate order. Am J Phys Anthropol 110:17–25.

In Old World monkeys such as macaques (genus *Macaca*) and baboons (genus *Papio*), interactions between adult females and infants are by no means limited to mother-offspring dyads. Although mothers provide most, if not all, of the care needed by infants, including nutrition, transport, and protection, females of all ages show a great deal of interest in other females' infants and spend a considerable amount of time interacting with them (Rowell et al., 1964; Hrdy, 1976). Interactions with other females' infants, collectively referred to as infant handling, are usually initiated by females and may include brief touching, holding, carrying, grooming, pulling, dragging, kidnapping, or aggression (Hrdy, 1976; Maestripieri, 1994a). In macaques, females begin infant handling when they are as young as a few months old, and by the end of the first year of life, there is already a clear sex difference in infant handling, with females being far more involved in this activity than males (Lovejoy and Wallen, 1988; Wallen et al., 1995). Newborn infants are usually the most attractive, and infant attractiveness to females decreases steadily with infant age (Alley, 1980; Maestripieri, 1994b; Treves, 1997).

Over the last 3–4 decades, a large number of studies have investigated infant handling at all levels of behavioral analysis, including ontogeny (Lancaster, 1971; Fairbanks, 1990), causation (Maestripieri and Wallen, 1995; Maestripieri and Zehr, 1998), adaptive function (Quiatt, 1979; Fairbanks, 1990; Small, 1990; Paul and Kuester, 1996), and evolution (Kohda, 1985; Mitani and Watts, 1997; Treves, 1997). One main issue that still remains unresolved at all four levels of

Grant sponsor: H.F. Guggenheim Foundation; Grant sponsor: NIMH; Grant number: MH57249; Grant sponsor: NIH; Grant number: RR-00165.

*Correspondence to: Dario Maestripieri, presently at the Human Development Committee, University of Chicago, 5730 S. Woodlawn Ave., Chicago, IL 60637. E-mail: dario@ccp.uchicago.edu

Received 26 March 1998; accepted 27 April 1999.

analysis is the exact nature of the relationship between infant handling and maternal behavior. In other words, it is not entirely clear whether infant handling represents an ontogenetic component of maternal behavior, whether it is regulated by the same internal factors and external stimuli as maternal behavior, whether it has an adaptive function similar to maternal behavior, different functions, or no function at all, and whether its evolution among Old World monkeys and other anthropoid primates has occurred independently from the evolution of maternal behavior.

In macaques, both maternal behavior and infant handling may include abusive interactions with infants. A recent study of rhesus macaques showed that, in addition to several differences in parenting and social behavior, abusive mothers interacted with other females' infants more frequently than nonabusive mothers during the third month of lactation (Maestripieri, 1998). The relationship between maternal abuse of one's own offspring and the quality of infant handling, however, was not investigated. Therefore, the question of whether maternal abuse of one's own offspring reflects a tendency to interact negatively with infants in general or a behavioral phenomenon specific to one's own offspring remains unanswered.

This study investigated infant abuse and the quality of infant handling in rhesus macaques, and it also tested several hypotheses concerning the relationship between maternal behavior and infant handling. To this end, the data set previously used to investigate the parenting and social behavior of rhesus abusive and nonabusive mothers was reanalyzed with particular focus on infant handling. For analysis purposes, infant handling was classified as harassment or aunting, depending on the quality of the interaction (see Methods).

Several contrasting predictions can be derived from the hypotheses that maternal abuse of offspring reflects a tendency to interact negatively with infants in general (hypothesis 1) or is a behavioral phenomenon specific to one's own offspring (hypothesis 2). Hypothesis 1 predicts that infant harassment is different between abusive and nonabusive mothers, and in particular, that abusive mothers are more likely to harass other females' infants than nonabusive mothers. It also predicts that individual differences in the frequency with which mothers abuse their offspring are positively correlated with individual differences in the frequency of infant harassment. Finally, according to hypothesis 1, we may also expect that variables such as maternal rank, maternal parity, offspring sex, and offspring age have different effects on infant harassment in abusive and nonabusive mothers. In contrast, hypothesis 2 predicts no significant differences in infant harassment between abusive and nonabusive mothers, no correlation between individual differences in abuse and harassment, and no differential effects of maternal rank, maternal parity, offspring sex, and offspring age on infant harassment in abusive and nonabusive mothers.

Several further hypotheses were formulated and tested to investigate the causation and function of infant handling and its relationship with maternal behavior in both abusive and nonabusive mothers. For example, if attraction to one' s own infant and attraction to other females' infants are mediated by similar mechanisms (e.g., the stimulus properties of young infants such as their body size, coat coloration, or behavior; Alley, 1980; Treves, 1997), then mothers are expected to increasingly seek out the young infants of other females as their own infants grow older and lose their attractiveness. Furthermore, if infant handling is just a by-product of maternal behavior with no adaptive function (Quiatt, 1979; Paul and Kuester, 1996), then infant harassment may be just an accidental by-product of infant handling. In other words, it is possible that when adult females interact with infants, a small proportion of these interactions will accidentally be rough and cause infant distress. Alternatively, infant harassment may be the result of female clumsiness or ineptitude. Thus, it is possible that experience gained with one's own offspring is reflected in the quality of interactions with other females' infants, and that females without previous maternal experience are more likely to hurt infants than maternally experienced females. Finally, infant harassment may be interpreted as a form of reproductive compe-

tition among lactating females (Silk, 1980; Wasser, 1983; Maestripieri, 1994a). In fact, assuming that harassment can decrease the chances of infant survival or impair the infants' present or future competitive abilities (see Maestripieri, 1994a), lactating females competing for resources are expected to harass each other's infants (Wasser, 1983).

The hypothesis that infant harassment is an accidental by-product of infant handling predicts that the percentage of infant handling episodes that constitute harassment should not vary significantly across individuals, irrespective of differences in the frequency of infant handling. The hypothesis that infant harassment is the result of female clumsiness and inexperience predicts no differences in infant harassment in relation to the frequency of infant handling but higher harassment among nulliparous mothers than among multiparous mothers. This hypothesis also predicts that the probability of harassment should decrease as a function of offspring age, particularly among nulliparous mothers, because maternal experience will presumably increase with offspring age. The hypothesis that infant harassment is a form of female reproductive competition predicts that infant harassment may differ in relation to the frequency of infant handling but not in relation to parity. Moreover, harassment should be more likely to occur when its benefits are higher and its costs are lower. Thus, harassment should be more beneficial to mothers of daughters than to mothers of sons because daughters are more likely than sons to remain in their natal group and compete for resources (Silk, 1983). Harassment of other infants should also remain constant or increase as a function of offspring age because the probability of infant survival usually increases with age (e.g., Rhine et al., 1988). Thus, offspring value increases with age and the prospective benefits of infant harassment will increase as well. Finally, harassment should be less costly to high-ranking mothers than to low-ranking mothers because the former are less likely to incur retaliation than the latter (Maestripieri, 1994c). Therefore, once rank-related differences in accessibility to infants are controlled, infant harassment should be more frequent among high-ranking than among low-ranking mothers.

It must be emphasized that the hypotheses that infant harassment is due to female clumsiness/inexperience or reproductive competition are not mutually incompatible and that they only apply to a subset of the interactions between mothers and other females' infants. Other hypotheses and explanations may be necessary to account for the occurrence of aunting. These two hypotheses also give rise to other predictions concerning the age, sex, and relatedness of the infants that are harassed, but these predictions could not be tested in this study because the necessary information was not available.

METHODS

Subjects and procedure

This study was conducted from March–August 1996 at the Field Station of the Yerkes Regional Primate Research Center (Lawrenceville, GA). At the beginning of the rhesus birth season, in March, ad libitum observations of four rhesus macaque groups were started. The groups were housed in adjacent outdoor compounds (35 $\times$ 35 m) with attached indoor quarters. Each group consisted of 2–5 adult males and 25–30 adult females with their subadult and juvenile offspring. All animals were fed twice a day and water was freely available. The criterion used to identify abusive mothers was the occurrence of one of the following behavior patterns: infant dragging, crushing, throwing, or sitting/stepping on (see below for definitions). These patterns are clearly distinguishable from other behaviors in the maternal and aggressive repertoire, such as those observed during mother-infant weaning conflicts. Ten abusive mothers were identified and served as subjects, while 10 mothers that were never observed to abuse their infants served as controls. Among abusive mothers, 3 were high-ranking, 4 middle-ranking, and 3 low-ranking. Eight of them were multiparous, and 2 were nulliparous. Six of their infants were male, and 4 were female. Among nonabusive mothers, 2 were high-ranking, 5 middle-ranking, and 3 low-ranking. Seven of them were multiparous, and 3 were nulliparous. Six of

their infants were male, and 4 were female (for further information on the identification of subjects and their characteristics, see Maestripieri, 1998).

Data collection and analysis

Focal observations of all mothers and infants were made during the first 12 weeks of infant life. Each mother-infant pair was observed in four weekly 30-min observation sessions, randomly distributed between 0800–1900 hr. Observations were made from a platform that provided an unrestricted view of the entire compound, and data were collected with a portable computer. Data collection and analysis included infant abuse and infant handling, which were defined as follows.

Infant abuse. The following maternal behavior patterns were included in the infant abuse category: 1) dragging: the mother drags her infant by its tail or leg while walking or running; 2) crushing: the mother pushes her infant on the ground with both hands; 3) throwing: the mother throws her infant a short distance with one hand while standing or walking; 4) hitting: the mother violently slaps her infant with one hand or arm; 5) biting: common definition; 6) stepping or sitting on: the mother steps on her infant with one foot or both feet, or sits on her infant; 7) dangling/dropping: the mother climbs a tree or fence and holds her infant by its tail or leg or drops her infant on the ground; and 8) rough grooming: the mother pulls her infant's hair or otherwise roughly grooms it, causing distress calls. Abuse events did not last more than a few seconds and therefore were recorded only in terms of their frequency. Infant abuse was recorded as two separate events if there was a transition in the pattern of behavior (e.g., from dragging to throwing) or if there was a pause of at least 10 sec during the behavior.

Infant handling. All interactions involving a physical contact between mothers and other females' infants (age 0–3 months) that were initiated by mothers were considered infant handling. Infant handling included both harassment and aunting. *Infant harassment* was scored when mothers pulled, dragged, hit, or bit other females' infants, causing infant distress calls. *Aunting* was scored when mothers touched, held, carried, or groomed other females' infants. The term aunting is used here without implying that these interactions were a form of caregiving behavior or otherwise beneficial to the infant. Infant handling episodes were usually very brief and were recorded only in terms of their frequency. For analysis purposes, the percentage of all infant-handling episodes classified as harassment (*percentage harassment*) was calculated. Percentage harassment was interpreted as an indicator of the quality of infant handling or of the mothers' tendency to harass other females' infants.

The frequencies of behavior recorded in the four weekly sessions were summed to obtain weekly scores, although most analyses were conducted using the total frequencies of behavior during the entire study period (24 hr of observation per individual). Data were analyzed with parametric statistics. Whenever the data failed to meet the assumptions necessary for the use of parametric tests (e.g., normality of distribution and homogeneity of variance), they were transformed by using square-root transformations in case of frequencies, and arcsine transformations for percentages. All tests were two-tailed, and probabilities (P) ≤ 0.05 were considered statistically significant.

RESULTS

Frequency and quality of infant handling in abusive and nonabusive mothers

The total number of handling episodes and the total number of aunting episodes were higher for abusive mothers than for controls (Student's t-test for unpaired samples: $t = 2.40$, df = 18, $P < 0.05$; aunting: $t = 2.31$, $P < 0.05$; Fig. 1). The total number of harassment episodes and the percentage of harassment episodes were not significantly different (harassment: $t = 1.78$, n.s.; percentage harassment: $t = 1.15$, n.s.; Fig. 1). Aunting and harassment data were also analyzed with a repeated-measures analysis of variance (ANOVA), which showed a main effect of the mother's identity (abusive vs. nonabusive: F 1, 18 = 5.77, $P < 0.05$) as well as an interaction between mother's identity and behavior (aunting vs. harassment: F 1,

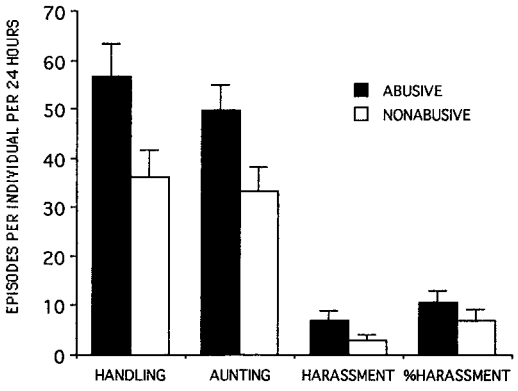

Fig. 1. Mean (± SEM) number of episodes of total infant handling, aunting, harassment, and percentage harassment per individual in abusive and nonabusive mothers. Data refer to the entire study period (24 hr of observation per individual).

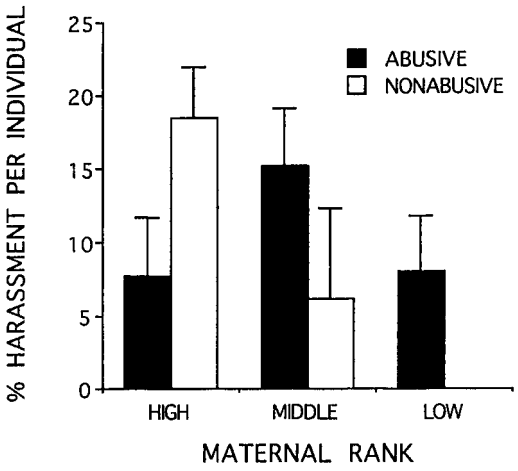

Fig. 2. Mean (± SEM) percentage of harassment episodes per individual in high-, middle-, and low-ranking abusive and nonabusive mothers. Data refer to the entire study period (24 hr of observation per individual).

18 = 4.42, $P = 0.05$). Taken together, these findings indicate that abusive mothers were more interested in other females' infants than were controls, but that their tendency to harass infants was similar to that of controls. Across all individuals, the percentage of harassment episodes was positively correlated with the total number of handling episodes (Pearson's correlation; R = 0.53, N = 20; $P < 0.05$). Therefore, the higher the frequency of infant handling, the higher the tendency to harass infants.

Effects of maternal rank, maternal parity, and offspring sex

To investigate whether maternal rank (high, middle, or low), maternal parity (nulliparous, multiparous), and offspring sex (male, female) affected infant handling and harassment and whether these effects were different for abusive and nonabusive mothers, 2 × 2 factorial ANOVAs were run for total number of handling episodes, total number of aunting episodes, total number of harassment episodes, and percentage of harassment episodes. The interest here was only in the effects of rank, parity, and offspring sex on infant-handling variables and their possible interaction with the mothers' identity (abusive vs. nonabusive), because main differences between abusive and nonabusive mothers had already been assessed.

There were no significant effects of rank alone or in interaction with the mothers' identity for total number of handling episodes (rank: F 2, 14 = 0.64, n.s.; rank × mothers' identity: F 2, 14 = 2.17, n.s.), total number of aunting episodes (rank: F 2, 14 = 0.98, n.s.; rank × mothers' identity: F 2, 14 = 2.68, n.s.), and total number of harassment episodes (rank: F 2, 14 = 0.73, n.s.; rank × mothers' identity: F 2, 14 = 1.63, n.s.). However, there was a main effect of rank on the percentage of harassment episodes (F 1, 14 = 4.60, $P = 0.05$), the percentage being higher for high-ranking than for low-ranking mothers (Bonferroni-Dunn post hoc test, $P = 0.05$). There was also a significant interaction between the effects of rank and mothers' identity on the percentage of harassment episodes (F 2, 14 = 4.52, $P < 0.05$), resulting from the fact that the highest scores were shown by high-ranking mothers among controls but by middle-ranking mothers among abusive mothers (Fig. 2). Taken together, these results indicate that maternal rank did not affect the total frequency of interactions with other females' infants, that high-ranking mothers had a higher tendency to harass infants than low-ranking mothers irrespective of infant accessibility, and that this effect of rank was more

marked among nonabusive mothers than among abusive ones.

Maternal parity and offspring sex had no significant effects on the four infant-handling variables, alone or in interaction with mothers' identity. Therefore, previous maternal experience and the sex of the current offspring had no influence on the frequency or the quality of interactions with other females' infants in abusive and nonabusive mothers.

Correlations between infant abuse and infant handling

Among the 10 abusive mothers, the total number of abuse episodes was positively correlated with the infant-handling variables, although none of the correlations reached statistical significance (Pearson's correlation; total number of handling episodes: R = 0.58, n.s.; total number of aunting episodes: R = 0.52, n.s.; total number of harassment episodes: R = 0.54; n.s.; percentage of harassment episodes: R = 0.32, n.s.).

Time course of infant handling in relation to offspring age and infant abuse

To investigate whether infant-handling variables showed differences between abusive and nonabusive mothers in relation to offspring age, repeated-measures ANOVAs were run, using the 12 weekly scores of aunting, harassment, and percentage harassment for abusive and nonabusive mothers. The interest here was in the effect of offspring age alone or in interaction with mothers' identity. There was a main effect of offspring age on both aunting ($F_{11, 198} = 13.29$, $P < 0.0001$) and harassment ($F_{11, 198} = 2.92$, $P = 0.001$), but no significant interaction with mothers' identity for either variable (aunting: $F_{1, 11} = 1.67$, n.s.; harassment: $F_{1, 11} = 1.13$, n.s.). Figure 3 shows that aunting increased steadily with offspring age, while harassment increased during the first 6 weeks and then leveled off. Similar results obtained with the total number of handling episodes were presented elsewhere (Maestripieri, 1998). It was not possible to run an ANOVA with the percentage harassment data because of too many missing data points (i.e., many individuals did not handle infants every week, particularly in the first month of lactation). However, the mean values of percentage harassment per week were not correlated with offspring age (R = 0.54, N = 12, n.s.). This was true also when only data for nulliparous mothers were analyzed (R = 0.17, N = 12, n.s.).

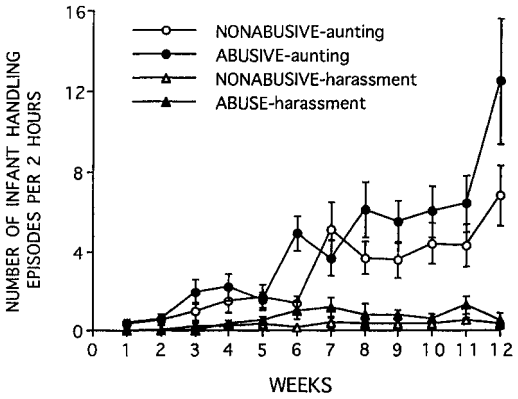

Fig. 3. Mean (± SEM) number of aunting and harassment episodes per individual per week (2 hr of observation) in abusive and nonabusive mothers during the first 12 weeks of lactation.

The relationship between offspring age, infant abuse, and infant handling was examined in more detail among abusive mothers. The number of abuse episodes was negatively correlated with offspring age in weeks (R = -89, N = 12, $P < 0.01$), whereas all infant-handling variables except percentage harassment were positively correlated with offspring age (total number of handling episodes: R = 0.92; $P < 0.01$; total number of aunting episodes: R = 0.90, $P < 0.01$; total number of harassment episodes: R = 0.69, $P < 0.05$; percentage harassment: R = 0.29, n.s.). Therefore, abusive mothers abused their own infants less frequently as infants grew older and gradually increased they frequency of both positive and negative interactions with other females' infants. However, the quality of these interactions, as measured by percentage of harassment, remained relatively constant.

DISCUSSION

Relationship between infant handling and infant abuse

Abusive mothers interacted with other females' infants more frequently than did

nonabusive mothers during the first 12 weeks of lactation. The frequency of aunting was higher for abusive than nonabusive mothers, whereas there were no significant differences in the frequency of harassment or the percentage of harassment episodes. These findings support hypothesis 2, that infant abuse is a phenomenon specific to one's own offspring and does not reflect a general tendency to interact negatively with infants. Hypothesis 2 was also supported by the lack of significant correlation between individual frequencies of infant abuse and infant harassment among abusive mothers. Because the correlation involved a relatively small number of individuals, however, this finding must be taken with caution. Consistent with hypothesis 2, there were no significant differences in the effects of maternal parity and offspring sex on infant-handling variables in abusive and nonabusive mothers. Moreover, among abusive mothers, infant abuse decreased as a function of offspring age, whereas the quality of infant handling remained relatively constant. The only inconsistency with hypothesis 2 was the finding that maternal rank affected infant harassment differently in abusive and nonabusive mothers, harassment being most frequent among high-ranking nonabusive mothers but not among abusive mothers. While the cause of this difference is not immediately clear, it might have more to do with differences in temperament between abusive and nonabusive mothers than in the nature of infant harassment. Among nonabusive mothers, harassment decreased as a function of dominance rank, perhaps due to the fact that lower-ranking females incur higher risk of retaliation from the infants' mothers than higher-ranking females. Although the relationship between dominance rank and risk of retaliation should be expected among abusive mothers as well, it is possible that the aggressive temperament and impulsivity of abusive females (Maestripieri, 1998) prompt them to harass infants, disregarding the potential responses of the infants' mothers. Aside from the differential effect of dominance rank, however, all of the other findings suggest that the tendency to harass other females' infants was similar between abusive and nonabusive mothers. Thus, abusive mothers showed greater interest in interacting with infants in general, and a higher frequency of positive, but not negative, interactions with them.

The findings of this study are consistent with the hypothesis that maternal abuse of offspring in rhesus macaques is causally related to the parenting styles of abusive mothers rather than to their inadequate responsiveness to infant stimuli (Troisi and D'Amato, 1994; Maestripieri, 1998). According to this hypothesis, abusive mothers find all infants (including their own) very attractive but, perhaps because of their high excitability and impulsivity, display high levels of control (defined as high levels of both maternal protectiveness and rejection) over their infant's activity (Maestripieri, 1998; Maestripieri and Carroll, 1998a). High levels of impulsivity and maternal control may increase the probability of infant abuse in individuals that are predisposed by their family's history (Maestripieri and Carroll, 1998b).

Causes and functions of infant handling and infant harassment in rhesus macaques

This study showed that rhesus macaque mothers with dependent infants actively seek the opportunity to interact with other females' infants. Moreover, as their own infants grow older, mothers increase the frequency with which they handle other infants. This finding is consistent with the hypothesis that maternal behavior and infant handling are regulated by similar proximate mechanisms, e.g., female characteristics (e.g., hormonal state, experience, temperament) and infant stimuli. Lactating females are probably in a high motivational state to interact with young infants (Pryce, 1992), and when their own infants lose some of their physical attractiveness with age, they turn their attention to other available infants in the group.

Infant harassment is not an accidental by-product of infant handling, because the percentage of harassment episodes increased with the frequency of handling. Moreover, infant harassment was more frequent among high-ranking mothers, whereas this was not

the case for infant handling. Infant harassment is not a by-product of maternal inexperience because nulliparous mothers did not harass infants more than multiparous mothers and because harassment did not decrease with increasing offspring age, as predicted by the inexperience hypothesis.

The effects of rank and offspring age on infant harassment are consistent with the hypothesis that this phenomenon reflects reproductive competition among lactating females. The association between high maternal rank and frequent infant harassment was predicted by the competition hypothesis because the costs of harassment (e.g., risk of retaliation) are probably lower to high-ranking than to low-ranking individuals. The lack of significant variation in the percentage of harassment episodes as a function of offspring age is also consistent with the competition hypothesis (see Introduction). The lack of significant effects of offspring sex on infant harassment, however, was not predicted by the competition hypothesis.

The prediction of the competition hypothesis tested in this study was that mothers with daughters should harass other infants more than mothers with sons. A more precise prediction of the competition hypothesis, however, could be that high-ranking mothers with daughters should harass the infant daughters of low-ranking mothers (Silk, 1983). It is possible that with information on the sex of the infants being harassed, this specific prediction could have been confirmed. Alternatively, it is possible that the effects of female reproductive competition on infant harassment are more apparent in wild populations, in which competition for resources is severe and infant mortality is high, than in captivity.

CONCLUSIONS

Although abuse of one's own offspring and harassment of other females' infants may be superficially similar, they are likely to be different phenomena with different causes and functions. Infant harassment cannot be explained as an accidental by-product of infant handling or maternal inexperience, but it is likely to have an adaptive function related to female reproductive competition. It is reasonable to hypothesize that maternal behavior and infant handling are regulated by similar mechanisms but serve different functions. Indeed, infant handling in itself is likely to serve multiple functions, beyond those investigated in this study. Further understanding of the adaptive functions of infant handling and its evolutionary relationship with maternal behavior could be gained by comparative analyses of these phenomena across the Old World monkeys and the entire Primate order.

ACKNOWLEDGMENTS

The Yerkes Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

LITERATURE CITED

Alley TR . 1980. Infantile coloration as an elicitor of caretaking behavior in Old World primates. Primates 21:416–429.

Fairbanks LA. 1990. Reciprocal benefits of allomothering for female vervet monkeys. Anim Behav 40:553–562.

Hrdy SB. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. Adv Stud Behav 6:101–158.

Kohda M. 1985. Allomothering behaviour of New and Old World monkeys. Primates 26:28–44.

Lancaster JB. 1971. Play mothering: the relations between juvenile females and young infants among free ranging vervet monkeys (*Cercopithecus aethiops*). Folia Primatol (Basel) 15:161–182.

Lovejoy J, Wallen K. 1988. Sexually dimorphic behavior in group-housed rhesus monkeys (*Macaca mulatta*) at 1 year of age. Psychobiology 16:348–356.

Maestripieri D. 1994a. Social structure, infant handling, and mothering styles in group-living Old World monkeys. Int J Primatol 15:531–553.

Maestripieri D. 1994b. Influence of infants on female social relationships in monkeys. Folia Primatol 63: 192–202.

Maestripieri D. 1994c. Costs and benefits of maternal aggression in lactating female rhesus macaques. Primates 35:443–453.

Maestripieri D. 1998. Parenting styles of abusive mothers in group-living rhesus macaques. Anim Behav 55:1–11.

Maestripieri D, Carroll KA. 1998a. Behavioral and environmental correlates of infant abuse in group-living pigtail macaques. Inf Behav Dev 21:603–612.

Maestripieri D, Carroll KA. 1998b. Risk factors for infant abuse and neglect in group-living rhesus monkeys. Psychol Sci 9:65–67.

Maestripieri D, Wallen K. 1995. Interest in infants varies with reproductive condition in group-living female pigtail macaques (*Macaca nemestrina*). Physiol Behav 57:353–358.

Maestripieri D, Zehr JL. 1998. Maternal responsiveness increases during pregnancy and after estrogen treatment in macaques. Horm Behav 34:223–230.

Mitani JC, Watts D. 1997. The evolution of non-maternal caretaking among anthropoid primates: do helpers help? Behav Evol Sociobiol 40:213–220.

Paul A, Kuester J. 1996. Infant handling by female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem: testing functional and evolutionary hypotheses. Behav Ecol Sociobiol 39:133–145.

Pryce CR. 1992. A comparative systems model of the regulation of maternal motivation in mammals. Anim Behav 43:417–441.

Rhine RJ, Wasser SK, Norton GW. 1988. An eight-year study of social and ecological correlates of mortality among immature baboons of Mikumi National Park, Tanzania. Am J Primatol 16:199–212.

Quiatt D. 1979. Aunts and mothers: adaptive implications of allomaternal behavior of nonhuman primates. Am Anthropol 81:310–319.

Rowell TE, Hinde RA, Spencer-Booth Y. 1964. "Aunt"-infant interaction in captive rhesus monkeys. Anim Behav 12:219–226.

Silk JB. 1980. Kidnapping and female competition among captive bonnet macaques. Primates 21:100–110.

Silk JB. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. Am Nat 121:56–66.

Small MF. 1990. Alloparental behaviour in Barbary macaques, *Macaca sylvanus*. Anim Behav 39:297–306.

Treves A. 1997. Primate natal coats: a preliminary analysis of distribution and function. Am J Phys Anthropol 104:47–70.

Troisi A, D'Amato FR. 1994. Mechanisms of primate infant abuse: the maternal anxiety hypothesis. In: Parmigiani S, vom Saal F, editors. Infanticide and parental care. London: Harwood. p 199–210.

Wallen K, Maestripieri D, Mann DR. 1995. Effects of neonatal testicular suppression with a GnRH antagonist on social behavior in group-living juvenile rhesus monkeys. Horm Behav 29:322–337.

Wasser SK. 1983. Reproductive competition and cooperation among female yellow baboons. In: Wasser SK, editor. Social behavior of female vertebrates. New York: Academic Press. p 349–390.